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Research Article

Community assembly shapes the performance of *Solanum nitidibaccatum*, an emerging ruderal non-native

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Abstract

A growing number of emerging non-native species are expanding within their introduced ranges and may become increasingly problematic in the future. Among them, several *Solanum* taxa pose underappreciated ecological and economic risks. *Solanum nitidibaccatum*, a poorly studied annual native to South America and increasingly recorded across Europe, represents a suitable model for understanding the establishment of non-native ruderal and segetal *Solanum* species in a transformed landscape. We examined how the composition and functional structure of ruderal vegetation influence the occurrence of *S. nitidibaccatum*, hypothesizing that habitat filtering and high functional heterogeneity facilitate its establishment, whereas interspecific competition constrains it. Using community diversity metrics and functional structure indices, we related vegetation properties to the probability of this species occurrence. The probability of *S. nitidibaccatum* occurrence was higher in species-rich communities and in vegetation characterized by higher leaf dry matter content and greater functional dispersion. In contrast, it declined in assemblages with a stronger contribution of nitrogen-demanding species and taller vegetation with higher specific leaf area. Our findings indicate that the establishment of *S. nitidibaccatum* is shaped by the interplay between habitat filtering and functional heterogeneity in ruderal vegetation, which may create underutilized niche space that facilitates the spread of this emerging non-native species. Considering its potential capacity to colonize ecologically similar vegetation across a range of transformed ecosystems, *S. nitidibaccatum* should be regarded as a species with high potential to become a problematic invasive weed. Its continued spread, together with the emergence of other non-native *Solanum* species, underscores the need for further research to better anticipate ecological and economic consequences that are challenging to predict.

Key words: Functional diversity, non-native annuals, ruderal vegetation, shiny berry nightshade, transformed landscape

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Introduction

In an era of diminishing geographical barriers, a defining feature of the Anthropocene epoch (Capinha et al. 2015; van Kleunen et al. 2015), the movement of organisms between continents has accelerated markedly. Plants are introduced both deliberately, for ornamental, practical, or agricultural use, and unintentionally, through seed contamination transported with soil, building materials, or agricultural machinery (Mack

et al. 2000). As a result, many species now occur thousands of kilometers beyond their native ranges (Keller et al. 2011). This trend is particularly important under ongoing climate warming, which facilitates the acclimatization and naturalization of species originating from warmer regions (Dullinger et al. 2017; Haeuser et al. 2019).

Although most introduced species fail to survive in new environments, some persist for many years in a lag phase, and others eventually spread and become naturalized (Richardson et al. 2000). The scale of introductions has turned this process into a major ecological challenge, particularly in light of the growing number of so-called 'emerging non-native species' that appear only sporadically but may become problematic in the future (Seebens et al. 2018; Pyšek et al. 2020). Once established, such species often colonize human-modified ecosystems and may expand beyond them (Potgieter and Cadotte 2020; Bayón et al. 2021; Hanberry 2023). Some ultimately develop into troublesome weeds, pests, or pathogens (Pyšek et al. 2012; Mollot et al. 2017; Gallardo et al. 2024). Many form dense stands in ruderal and arable habitats and become characteristic elements of the local flora, promoting the emergence of novel ecosystems (Hobbs et al. 2009; Steffen et al. 2015).

The genus *Solanum* L. offers a clear illustration of a taxonomic group containing numerous non-native species. Well-known examples include *S. nigrum* L., *S. elaeagnifolium* Cav. (Roberts and Florentine 2022), *S. carolinense* L. (Follak and Strauss 2010), and *S. pimpinellifolium* L. (Knapp 2018). From several other *Solanum* species (e.g., *S. pimpinellifolium*, *S. torvum* Sw., *S. triflorum* Nutt.) that are now being reported with increasing frequency in Central Europe (Schmitz 2003; Knapp 2018; Musarella 2020), *S. nitidibaccatum* Bitter deserves particular focus. Although *S. nitidibaccatum*, native to temperate regions of western South America, is a common field weed in many parts of the world (Fig. 1), its biology and ecology remain poorly understood. This reflects both limited knowledge of the species in its native and introduced ranges and the fact that, outside its native range, it has frequently been misidentified as *S. physalifolium* Rusby (sporadically recorded outside South America) or *S. sarrachoides* Sendtn. (rare weed in Europe; Edmonds 1986; Knapp et al. 2023). As a result, much of the research on the biology and invasiveness of *S. physalifolium* and *S. sarrachoides* conducted outside South America actually refers to naturalized *S. nitidibaccatum*, which is widespread in Australia, New Zealand, western Canada, the United States, and Europe (Fig. 1; Särkinen et al. 2015, 2018; Knapp et al. 2019, 2020, 2023). The exact date of the introduction of *S. nitidibaccatum* to Europe is unknown. The earliest studies documenting its presence as an adventive weed date from the mid-20th century from France, Germany, and Fennoscandia (Haudricourt 1946; Militzer 1964; Saarisalo-Taubert 1967; Lang 1974).

Solanum nitidibaccatum is now naturalized in Spain, Belgium, and Luxembourg and has also been recorded in Albania, France, Greece, Germany, and Sweden (Valdés 2006). Further records come from Austria (Knapp 2018), Italy (Capuano and Caruso 2023), and Russia (Puzyrjov 2006), as well as from the Czech Republic, the United Kingdom, and the Netherlands, where it has often been reported as *S. physalifolium* (van Ooststroom and Reichgelt 1964; Silverside 1977). It is listed as an invasive taxon, under the name *S. physalifolium* var. *nitidibaccatum* (Bitter) Edmonds, in the European Alien Species Information Network (EASIN). Although the POWO database (2025) does not list the species for Poland, it has likely been present for some time but misidentified as *S. physalifolium* or *S. sarrachoides*, both included in the national checklist (Mirek et al. 2020). The presence of *S. nitidibaccatum* in Poland has been confirmed by Kobierski et al. (2022).

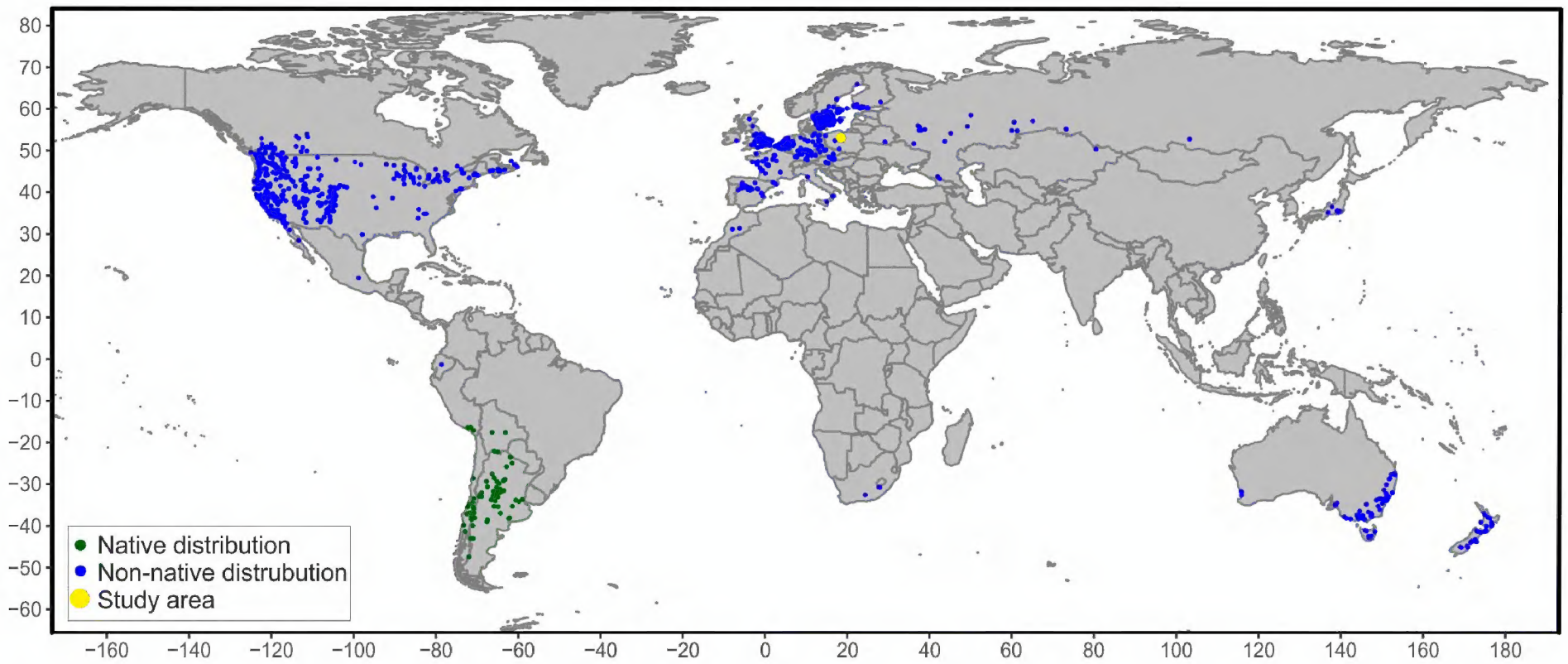

Figure 1. Distribution of *Solanum nitidibaccatum* based on records from the Global Biodiversity Information Facility (GBIF 2025, https://doi.org/10.15468/dl.7n47wt) and iNaturalist (www.inaturalist.org; accessed 3 Nov 2025). Green circles indicate occurrences within the native range, blue circles represent occurrences outside the native range, and the yellow circle marks the study site located outside the native range.

The late phenology of *S. nitidibaccatum* reflects its warm-climate affinity (Suppl. material 1) and its high thermal requirements for germination (Del Monte and Tarquis 1997; Taab 2009; Taab and Andersson 2009). Thus, ongoing climate warming is likely to enhance its ability to spread, increasing the risk that it will become a problematic weed, as documented for *S. nigrum* (Taab 2021), *S. carolinense* (Follak and Strauss 2010; Follak 2020; Follak et al. 2023), and *S. elaeagnifolium* (Roberts and Florentine 2022; Tataridas et al. 2022, 2023). Similarly to several other species of the genus *Solanum*, *S. nitidibaccatum* may constitute a substantial threat to economically important crops. It can carry the same pathogens as other problematic *Solanum* weeds, including *Phytophthora infestans* (Mont.) de Bary and *Meloidogyne fallax* Karsen, and it may also introduce additional pathogens capable of infecting potato (*S. tuberosum* L.) and tomato (*S. lycopersicum* L.) crops (Andersson et al. 2003; Deahl et al. 2005, 2006; Grünwald and Flier 2005; Olanya et al. 2005, 2009; Shah et al. 2010; Abreha 2017). *Solanum nitidibaccatum* can also hybridize with closely related species, most notably with *S. nigrum*, with which it forms the hybrid *S.* × *procurrens* A. C. Leslie recorded in Great Britain, Sweden, the Czech Republic, Russia, and New Zealand, regions where both parental species are recognized as invasive (Edmonds 1981; Puzyrjov 2006). In view of the documented but still underappreciated risks posed by *Solanum* species invasions, it is essential to improve our understanding of their ecology. In this context, *S. nitidibaccatum* serves as a model species, potentially reflecting the behavior of other non-native, ruderal, and segetal *Solanum* taxa in the future (Edmonds 1981; Olanya et al. 2005, 2009; Puzyrjov 2006; Abreha 2017; Vetukuri et al. 2020).

One tool for improving our understanding of non-native species establishment is the functional diversity (FD) approach, which enables inference on community assembly processes shaping species coexistence and invasion success (Czortek et al. 2023; Renault et al. 2023; Puchałka et al. 2025). Functional traits reflect species' life-history strategies and resource-use patterns, providing a mechanistic basis for assessing how recipient communities influence invader performance (Dyderski and

Jagodziński 2018; Palma et al. 2021; Kaushik et al. 2022). For instance, habitat filtering may promote the establishment of non-native species whose functional traits match the abiotic conditions of the recipient ecosystem, resulting in functional similarity between non-native and resident species (El-Barougy et al. 2020; Czortek et al. 2024). In contrast, interspecific competition may constrain establishment when non-native species are functionally similar to dominant residents because of increased niche overlap and resource competition (Borges et al. 2019; Divíšek et al. 2025). Under this perspective, communities characterized by high functional heterogeneity may facilitate invasion by reducing competitive exclusion and allowing functionally distinct non-native species to occupy underutilized niche space (Gallien and Carboni 2017; Cavieres 2021; Puchałka et al. 2025). Phylogenetic diversity often complements the FD approach in assessing the ecological success of non-native plant species (Cadotte et al. 2009; Galland et al. 2019). High phylogenetic similarity between non-native and resident species may intensify competition through phenological overlap (Ordonez 2014; Park et al. 2024). On the contrary, phylogenetically heterogeneous communities may reduce temporal niche overlap and increase opportunities for establishment of non-native species, particularly those with shifted or late phenology (Wolkovich and Cleland 2011; Godoy and Levine 2014).

In this study, we ask how the composition and community structure of ruderal vegetation influence the performance of emerging non-native *S. nitidibaccatum* in a transformed landscape. We hypothesize that its ecological success depends on community assembly processes within recipient vegetation, with habitat filtering and high functional and phylogenetic heterogeneity acting as dominant drivers promoting its establishment, while interspecific competition serves as a constraining driver limiting its occurrence.

Methods

Studied species

For many years, the taxonomy of *S. nitidibaccatum* remained unclear because it was widely treated as *S. physalifolium* var. *nitidibaccatum*. This long-standing misplacement blurred our understanding of the ecology and distribution of both species. Recent DNA-based revisions have demonstrated that *S. nitidibaccatum*, *S. physalifolium*, and *S. sarrachoides* are all distinct and not closely related (Särkinen et al. 2013, 2015, 2018; Knapp et al. 2019, 2020, 2023; Särkinen and Knapp 2022).

Solanum nitidibaccatum belongs to the Morelloid clade, a group of South American annual herbs that includes several field and ruderal weeds now established far beyond their native range (Särkinen et al. 2015; Knapp et al. 2023). In its native range in Argentina and Chile, the species occupies open sites, croplands, ruderal habitats, and drying riverbeds (Särkinen et al. 2015; Knapp et al. 2023). It is a taprooted therophyte, usually 10–90 cm tall, with ovate leaves that are entire or gently serrated and taper at the base. Leaves, stems, and calyces bear fine glandular hairs. The inflorescences carry up to seven white flowers, and the fruit is a marbled, poisonous berry partly enclosed by the calyx and containing one to three seeds.

Solanum nitidibaccatum is primarily distinguished from *S. physalifolium* and *S. sarrachoides* by its greenish-brown berries with white marbling and a strongly adhering calyx that covers up to half of the fruit. In *S. physalifolium*, the berries

are green with white marbling, but the calyx is conspicuous and does not adhere to the fruit. In contrast, *S. sarrachoides* also has a strongly adhering calyx, which covers a larger proportion of the berry than in *S. nitidibaccatum*, and its fruits are consistently uniformly green. A diagnostic floral character of *S. nitidibaccatum*, distinguishing it from the other two species, is the presence of darkly pigmented spots (typically U-shaped) located in the interveinal sinuses at the base of the corolla. In both *S. sarrachoides* and *S. physalifolium*, the corolla center is uniformly green or yellow-green and lacks such pigmentation. Vegetatively, *S. nitidibaccatum* has broadly ovate leaves with glandular trichomes. *Solanum sarrachoides* is characterized by more delicate, usually ovate leaves that are often oppositely arranged and by plants that are lax and softly pubescent. *Solanum physalifolium* bears ovate to elliptic leaves with denser and longer glandular trichomes than those of *S. nitidibaccatum* (Särkinen et al. 2015; Knapp et al. 2023).

Study area and study design

We carried out the study in northern Poland, in the city of Toruń and the surrounding area (Fig. 2). Three of the most abundant populations of *S. nitidibaccatum* recorded in 2023 were selected for this study. Two were located within Toruń and one in the village of Górsk, about 7.5 km from the city. All sites had been heavily disturbed by ongoing road reconstruction and supported vegetation dominated by segetal and ruderal species of the orders *Papaveretalia rhoeadis* Hüppe & Hofmeister ex Theurillat et al., *Sisymbrietalia* J. Tx. ex Görs, and *Onopordetalia acanthi* Br.-Bl. & Tx. ex Klika & Hadač (Ratyńska et al. 2010).

The Górsk population (Fig. 2: Site 1) grew along a roadside in a rural landscape, on freshly disturbed soil beside a new bicycle path, bordered by crop fields, meadows, and a small settlement with gardens and an abandoned orchard. In Toruń, one site was located in the city center and had a suburban wasteland character (Fig. 2: Site 2). *Solanum nitidibaccatum* grew there on sandy urbanosols rich in construction debris and household waste, and the vegetation developed spontaneously after the land was abandoned. It was composed mainly of nitrophilous ruderal species together with ornamental plants that had escaped from nearby gardens and a cemetery. The third site represented the most heavily transformed habitat (Fig. 2: Site 3), embedded within dense urban fabric comprising major transport infrastructure, workplaces, and mixed residential housing. Here the species was restricted to disturbed, infrequently managed sandy roadsides within intensively maintained urban greenery.

Due to the late phenology of *S. nitidibaccatum*, we carried out the vegetation survey in mid-September 2023, when most plant species were at an optimal phenological stage. We established 78 vegetation plots of 1 × 1 m, placing 39 plots in areas where *S. nitidibaccatum* occurred and 39 control plots where the species was absent. We established 22 plots in Site 1, 32 in Site 2, and 24 in Site 3 (Fig. 2). We recorded all vascular plant species and estimated their cover with the Braun-Blanquet scale, which we later converted to van der Maarel's nine-point ordinal scale. We selected the plots to address the range of local environmental conditions at each site and matched the control plots as closely as possible to the plots occupied by *S. nitidibaccatum* in habitat type, level of transformation, and disturbance. Species nomenclature follows the Euro+Med PlantBase checklist.

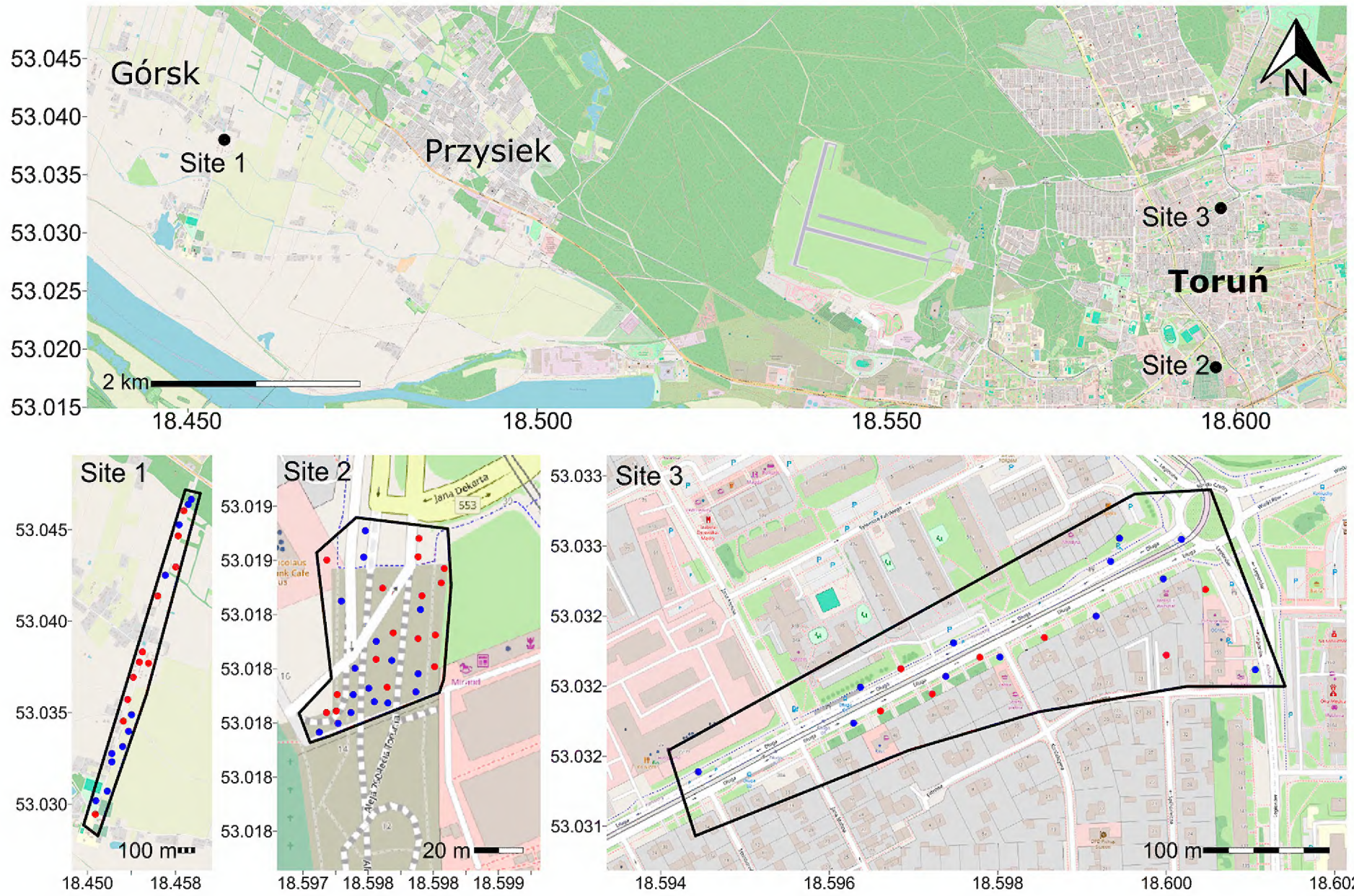

Figure 2. Location of the three study sites and the distribution of vegetation plots. Site 1 – rural landscape; Site 2 – suburban landscape; and Site 3 – urban landscape. Blue circles indicate plots where *S. nitidibaccatum* was present, while red points indicate control plots where the species was absent. Base maps are obtained from OpenStreetMap contributors (https://www.openstreetmap.org/copyright) and © Esri, Maxar, Earthstar Geographics, and CNES/Airbus (2025).

Vegetation traits

We analyzed data using R 4.3.1 (R Core Team 2025). To describe the gradients of environmental conditions preferred by plant species co-occurring with *S. nitidibaccatum*, we relied on ecological indicator values (EIV) for light (EIV-L), temperature (EIV-T), moisture (EIV-M), and soil fertility (EIV-N), following Ellenberg and Leuschner (2010). These values, developed by vegetation ecologists, are widely used to infer species' environmental niches when direct measurements are not available, which explains their frequent application in vegetation studies (e.g., Diekmann et al. 2019; Charmillot et al. 2021; Kammer et al. 2022). Although their categorical character and dependence on expert assessment have been noted as important limitations (Schaffers and Sýkora 2000), comparisons with experimental data have repeatedly shown that they provide a robust approximation of species' ecological requirements (Dzwonko 2001; Szymura et al. 2014).

To assess the gradients in the structure of functional traits of plant assemblages co-occurring with *S. nitidibaccatum*, for each vegetation plot we compiled data on eight plant traits obtained from the LEDA (Kleyer et al. 2008), BIEN (Enquist et al. 2016), BiolFlor (Kuhn et al. 2004), and Pladias (Chytrý et al. 2021) databases. Traits linked to the leaf economic spectrum, such as specific leaf area (*SLA*; $cm^2\ g^{-1}$) and leaf dry matter content (LDMC; $mg\ g^{-1}$), together with characteristics reflecting plant size, including canopy height (m) and life form (treated as a categorical

trait), provide information on species' competitive capacities by showing differences in resource acquisition and allocation strategies. We also used traits associated with dispersal and reproductive biology, including seed mass (mg), the onset and duration of flowering (months), and the predominant pollination mode (insect, wind, and self-pollination). These variables provide a basis for assessment of species' reproductive strategies, dispersal potential, persistence mechanisms, and their responses to habitat filters (Westoby 1998; Grime 2006; Díaz et al. 2016).

Because the initial dataset of plant species characteristics contained missing entries (Table 1), we imputed the missing values. We built a phylogenetic tree for all recorded taxa using the megatree from the *V.Phylo.maker* package (Jin and Qian 2019) and combined it with available trait data, EIVs, and phylogenetic eigenvectors generated using the *PVR* package (Diniz-Filho et al. 1998; Santos 2025). Missing values were then estimated with a random forest algorithm implemented in the *missForest* package, following Penone et al. (2014). The first 15 phylogenetic eigenvectors explained 70.21% of the variation in phylogenetic distances. The normalized RMSE for continuous traits was 0.334, and the misclassification error for categorical traits was 0.419, which is consistent with the accuracy reported in comparable studies (e.g., Penone et al. 2014; Czortek 2023; Czortek et al. 2025). Based on the imputed dataset, we subsequently calculated community weighted means (CWM) of EIVs, SLA, LDMC, seed mass, and canopy height for each vegetation plot.

Plant diversity metrics

To characterize how the performance of *S. nitidibaccatum* shifts along community diversity and assembly gradients, we used a set of taxonomic, phylogenetic, and functional diversity (FD) metrics. To describe the taxonomic diversity of plant species, we quantified species richness for each vegetation plot. To characterize

Table 1. Summary of trait characteristics used in the study, including their ranges, standard deviation (SD), and completeness.

Numeric traits	**Min**	**Max**	**Mean**	**SD**	**Completeness [%]**
Flowering beginning [months]	1.000	7.000	5.446	1.268	82.786
Flowering duration [months]	2.000	12.000	4.535	1.931	82.786
Canopy height [m]	0.200	10.000	1.138	1.101	82.786
Seed mass [mg]	0.056	35.336	2.570	5.536	80.327
Leaf dry mass content [mg g^{-1}]	84.000	514.700	194.400	65.954	73.770
Specific leaf area [cm^2 g^{-1}]	122.800	552.000	270.500	85.965	77.049
Light EIV	5.000	9.000	7.248	0.921	82.786
Temperature EIV	2.000	8.000	5.938	0.891	65.573
Moisture EIV	2.000	8.000	4.733	1.149	73.770
Soil fertility EIV	1.000	9.000	6.183	1.933	76.229
Categorical traits	**Number of classes**	**Classes and their frequency**			**Completeness [%]**
Life form	6	Chamaephytes (1.639%), Geophytes (3.279%), Hemicryptophytes (37.704%), Lianas (7.378%), Phanerophytes (0.819%), Therophytes (31.967%)			82.786
Pollination mode – insect	2	yes (63.115%), no (18.852%)			81.967
Pollination mode – self	2	yes (50.000%), no (31.967%)			81.967
Pollination mode – wind	2	yes (23.771%), no (58.196%)			81.967

the evolutionary structure of species assemblages, we calculated the mean pairwise phylogenetic distance (MPPD) for each vegetation plot, using the *PhyloMeasures* package (Tsirogiannis and Sandel 2016) and a phylogenetic tree generated through the *V.PhyloMaker* package (Jin and Qian 2019). MPPD measures the average evolutionary dissimilarity among all species pairs within a community. It is calculated based on branch lengths on the phylogenetic tree and reflects how closely or distantly related the co-occurring species are. Higher values indicate a more dissimilar phylogenetic structure (high phylogenetic diversity), whereas lower values point to clustering (low phylogenetic diversity). To account for the effect of species richness on phylogenetic diversity estimates, we standardized the MPPD.

To assess how fundamental ecological processes influence species composition and community assembly, we quantified four FD metrics for each vegetation plot using the FD package (Laliberté and Legendre 2010). Both numerical and categorical functional traits were used to calculate the FD indices using Gower distance, which allows the integration of mixed data types and the joint analysis of continuous and categorical traits. Functional richness (FRic) describes the span of functional strategies present in a community and the degree to which species fill the available niche space (Villéger et al. 2008). Functional evenness (FEve) characterizes how uniformly traits are distributed within this occupied space (Mason et al. 2005; Mouchet et al. 2010). Functional dispersion (FDis) and functional divergence (FDiv) represent mean differences among species in multivariate trait space, the former measured relative to the centroid and the latter reflecting how strongly species deviate from the central region. As a result, FDiv is more sensitive to species with extreme traits, whereas FDis is less influenced by them (Mason et al. 2005; Villéger et al. 2008; Pla et al. 2012). Low values of FD metrics often point to habitat filtering or strong competitive constraints, while high values are commonly associated with niche differentiation (high functional heterogeneity) that structures community assembly (Czortek et al. 2021b).

To eliminate the influence of species richness on estimates of FD metrics, we used the standardization approach provided by Czortek et al. (2021b). For each vegetation plot, a null model was generated by randomizing species composition with the *picante::randomizeMatrix()* function across 999 iterations (Kembel et al. 2010). Standardized effect sizes (SES) for all four FD metrics (FRic, FDis, FDiv, and FEve) were then computed using the formula: FDSES = (FDR – FDnull) / SD(FDnull), where FDR is the observed metric value, FDnull is the mean value of the null distribution, and SD(FDnull) represents its standard deviation.

Statistical analyses

We applied non-metric multidimensional scaling (NMDS) to characterize species assemblages and to identify the dominant gradients in plant species composition using the *vegan::metaMDS* function (Oksanen et al. 2025). NMDS was based on the default transformation settings and a Bray–Curtis dissimilarity matrix. To interpret the ecological meaning of NMDS1 and NMDS2 ordination axes, we examined how the major environmental and community attributes aligned with the distribution of plots in the ordination space by passively fitting landscape type and vegetation characteristics, including CWMs of EIVs and plant functional traits, as well as plant species diversity metrics using the *vegan::envfit()* function (Oksanen et al. 2025). We evaluated the significance of this fit with a permutation test involving 999 iterations.

We examined how the probability of *S. nitidibaccatum* occurrence varied along CWM gradients derived from EIVs, plant functional traits, and the main components of community diversity and assembly by fitting three generalized linear mixed-effect models (GLMM) with a binomial distribution of the response variable. To assess the performance of *S. nitidibaccatum* across the three groups of ecological gradients, we fitted separate global GLMMs for each gradient type. Landscape type was included as a random effect to account for spatial clustering of vegetation plots nested within the three study sites. This random effect also reflected fine-scale heterogeneity within the urban matrix, including variation in land-use composition and broad differences in urbanization intensity among landscape categories.

The model representing the EIV-based environmental gradients included EIV-L, EIV-T, EIV-M, and EIV-N as fixed effects. The model describing plant functional trait gradients included CWMs of seed mass, canopy height, SLA, and LDMC. The model representing community diversity and assembly gradients included species richness, MPPD, and SES of FRic, FDis, FDiv, and FEve. To examine collinearity among predictors, we calculated variance inflation factors (VIF) for each global GLMM using the *car::vif* function, adopting a threshold of five as an indication of substantial collinearity (Fox et al. 2024). None of the predictors exceeded this threshold in any of the three global GLMMs. To identify the final GLMMs with the strongest predictive ability for explaining the performance of *S. nitidibaccatum* across the three ecological gradient groups, we applied the model selection procedure in the *MuMIn* package (Bartoń 2017) and selected all model combinations with ΔAICc values below two. Based on this subset of top-ranked models, we then constructed a final GLMM for each gradient type by including all predictors present in the selected models (Suppl. material 2). We calculated marginal and conditional coefficients of determination (R^2m and R^2c) for all final models using the *MuMIn::r.squaredGLMM* function (Bartoń 2017), which quantifies variance explained by fixed effects alone and by both fixed and random effects, respectively. We did not use *p*-values to assess the strength of model results, as their sensitivity to sample size may obscure ecologically relevant effects (Wasserstein and Lazar 2016). To visualize model predictions, we derived marginal responses with the *ggeffects::ggpredict()* function (Lüdecke 2018; Lenth 2024), which estimate expected values while holding all other predictors at their average levels.

Results

The composition of ruderal plant communities formed two gradients in the NMDS ordination space, reflecting a compositional continuum across landscape types, community diversity and assembly, and species' environmental requirements and functional traits, as well as assemblages differing in the presence of *S. nitidibaccatum* (Table 2, Fig. 3, Suppl. material 3). Along the NMDS1 axis, plots with higher species richness and SES of FEve were separated from those characterized by greater seed mass and LDMC CWMs. The NMDS2 axis distinguished plots with higher soil moisture and fertility requirements (CWMs of EIV-M and EIV-N, respectively), together with greater canopy height CWM and SES of FRic, from those with higher light and temperature requirements (CWMs of EIV-L and EIV-T, respectively), higher SLA CWM, and greater phylogenetic and functional diversity (MPPD and SES of FDiv and FDis).

All parameters of the final GLMMs are presented in Table 3. Across all three GLMMs, the random effect of landscape type did not influence the probability of

Table 2. The result of the passive fit of vegetation characteristics and landscape type to non-metric multidimensional scaling ordination along NMDS1 and NMDS2 axes evaluated using a permutation test. Abbreviations: CWM – community-weighted mean, EIV – ecological indicator value, SES – standardized effect size. Statistically significant results are in bold.

Variable	Acronym	NMDS1	NMDS2	R^2	*P*
Ellenberg's ecological indicator-derived environmental CWM gradients:					
Light EIV CWM	EIV.L	0.624	0.780	0.136	**0.005**
Temperature EIV CWM	EIV.T	0.761	0.648	0.313	**0.001**
Soil moisture EIV CWM	EIV.M	–0.373	–0.927	0.037	0.236
Soil fertility EIV CWM	EIV.N	0.134	–0.991	0.018	0.528
Plant functional trait CWM gradients:					
Canopy height CWM [m]	C.height	–0.149	–0.988	0.309	**0.001**
Seed mass CWM [mg]	S.mass	0.999	0.016	0.068	**0.049**
Specific leaf area CWM [$cm^2\ g^{-1}$]	SLA	0.142	0.989	0.114	**0.010**
Leaf dry matter content CWM [$mg\ g^{-1}$]	LDMC	0.977	–0.210	0.198	**0.001**
Community diversity and assembly gradients:					
Species richness	Rich	–0.916	–0.399	0.372	**0.001**
Mean pairwise phylogenetic distance	MPPD	–0.446	–0.894	0.051	0.147
Functional richness SES	SESFRic	–0.412	–0.911	0.001	0.957
Functional dispersion SES	SESFDis	0.876	0.482	0.095	**0.031**
Functional divergence SES	SESFDiv	0.150	0.988	0.075	0.054
Functional evenness SES	SESFEve	–0.998	–0.057	0.026	0.367
Landscape type = rural	–	–0.167	–0.321	0.320	0.001
Landscape type = suburban	–	–0.088	0.080		
Landscape type = urban	–	0.271	0.187		

S. nitidibaccatum occurrence. The final GLMM assessing the effects of Ellenberg's EIV-derived environmental gradients revealed that the probability of *S. nitidibaccatum* occurrence increased with higher CWMs of light (from 33% at 6.6 to 65% at 8.0; Fig. 4A), temperature (from 28% at 5.4 to 78% at 7.2; Fig. 4B), and moisture (from 6% at 4.1 to 95% at 5.3; Fig. 4C) EIVs. In contrast, it declined with increasing soil fertility EIV CWM (from 89% at 5.2 to 16% at 7.2; Fig. 4D).

The final GLMM including plant functional trait CWM gradients showed that the probability of *S. nitidibaccatum* presence was lower in plots with higher CWMs of canopy height (from 76% at 0.4 m to 20% at 2.0 m; Fig. 4E), seed mass (from 74% at 0.5 mg to 9% at 15.0 mg; Fig. 4F), and SLA (from 74% at 210.0 $cm^2\ g^{-1}$ to 9% at 355.0 $cm^2\ g^{-1}$; Fig. 4G). It was, however, higher in plots characterized by greater LDMC CWM values (from 24% at 140.0 $mg\ g^{-1}$ to 72% at 250.0 $mg\ g^{-1}$; Fig. 4H).

Regarding the final GLMM testing the effects of community diversity and assembly gradients, the probability of *S. nitidibaccatum* occurrence was higher in more species-rich plots, increasing from 23% at six species to 87% at 23 species (Fig. 4I). At the same time, it decreased with increasing phylogenetic diversity (MPPD index), from 82% at –3.0 to 25% at 0.5 (Fig. 4J). The probability of *S. nitidibaccatum* presence decreased with increasing FRic SES (from 61% at –3.0 to 36% at 2.5; Fig. 4K), FDiv SES (from 77% at 5.0 to 34% at 2.0; Fig. 4L), and FEve SES (from 70% at –2.0 to 19% at 4.0; Fig. 4M), but increased with increasing FDis SES (from 24% at –2.5 to 64% at 1.5; Fig. 4N).

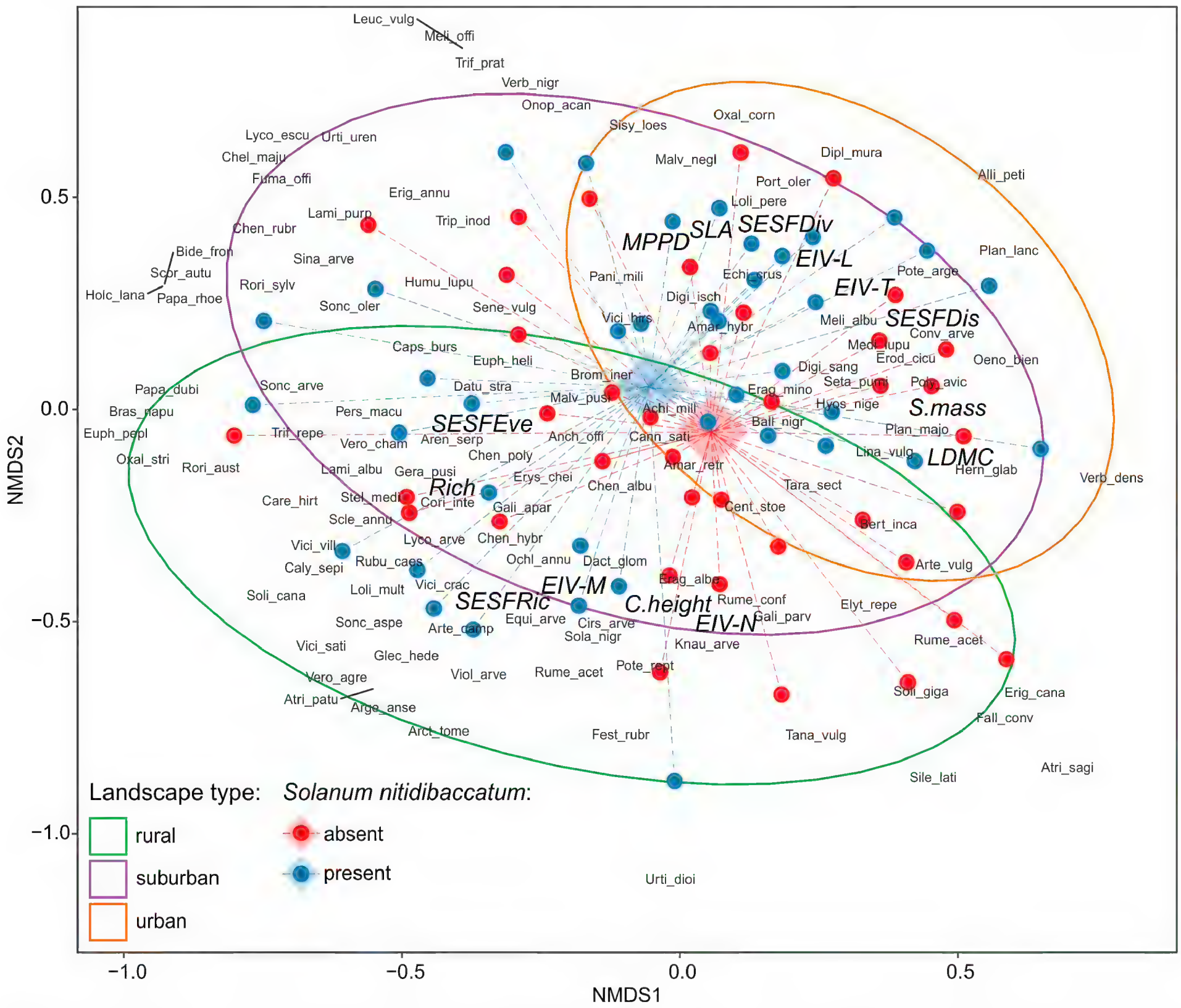

Figure 3. Result of non-metric multidimensional scaling (NMDS) ordination based on vegetation plots (dots, $n = 78$), colored by presence or absence of *S. nitidibaccatum*, and illustrating differences in species composition among three landscape types (shown as ellipses with a 95% confidence level). Diamonds and dashed lines represent centroids and distances from centroids for plots with and without *S. nitidibaccatum*. Black labels indicate passively fitted vegetation characteristics, explaining dissimilarities in species composition among plots (for the goodness of fit, see Table 2). Nine-digit acronyms denote plant species coordinates (for full species names, see Suppl. material 3).

Discussion

Non-native ruderal species co-occurs with stress-tolerant plants but not competitors

Our findings indicate that the performance of *S. nitidibaccatum* may be driven by the interplay of multiple abiotic and biotic gradients structuring the species composition of surveyed ruderal vegetation. This non-native ruderal occurred most often in communities dominated by light-demanding and thermophilous taxa, where reduced competition for light could coincide with strong physiological constraints imposed by intense insolation and high temperature extremes (Bokwa et al. 2020; Mogîldea and Biță-Nicolae 2024). Such conditions could only be tolerated by species with effective mechanisms for buffering environmental stress, although the severity of these extremes may have been mitigated by soil moisture (Guo et al. 2018; Zandalinas et al. 2018). The probability of occurrence of *S. nitidibaccatum* increased with the

Table 3. Parameters of the three final generalized linear mixed-effect models, selected using AICc (Suppl. material 2), predicting the probability of *S. nitidibaccatum* occurrence based on Ellenberg's ecological indicator-derived environmental gradients (R^2m and R^2c = 0.170), plant functional trait gradients (R^2m and R^2c = 0.175), and community diversity and assembly gradients including landscape type (R^2m and R^2c = 0.212). Variance and SE of the random effect were estimated as zero in all models. Abbreviations: CWM – community-weighted mean, EIV – ecological indicator value, SES – standardized effect size. Statistically significant results are in bold.

Variable	Estimate	SE	*z*	*Pr*(>|*z*|)
Ellenberg's ecological indicator-derived environmental CWM gradients:				
Fixed effects:				
(Intercept)	–24.376	14.520	–1.679	0.093
Light EIV CWM	0.937	1.036	0.904	0.365
Temperature EIV CWM	1.207	1.048	1.152	0.249
Moisture EIV CWM	4.706	1.870	2.517	**0.011**
Nitrogen EIV CWM	–1.894	0.883	–2.145	**0.032**
Plant functional trait CWM gradients:				
(Intercept)	4.726	5.191	0.910	0.363
Canopy height CWM [m]	–1.556	0.812	–1.917	0.053
Seed mass CWM [mg]	–0.511	0.428	–1.196	0.231
Specific leaf area CWM [$cm^2\ g^{-1}$]	–0.022	0.012	–1.827	0.067
Leaf dry matter content CWM [$mg\ g^{-1}$]	0.018	0.016	1.177	0.239
Community diversity and assembly gradients:				
Species richness	0.182	0.076	2.392	**0.017**
Mean pairwise phylogenetic distance	–0.741	0.337	–2.193	**0.028**
Functional richness SES	–0.186	0.259	–0.719	0.472
Functional dispersion SES	0.438	0.326	1.344	0.179
Functional divergence SES	–0.262	0.240	–1.092	0.274
Functional evenness SES	–0.378	0.240	–1.579	0.114

contribution of moisture-demanding species, suggesting that this species may exploit microsites where irregular water availability temporarily offsets irradiance, thermal, or evaporative stress. Similarly, within its natural range, it occurs in environments with periodically high water availability, such as along water margins or in temporarily drying riverbanks and streambeds (Särkinen et al. 2015; Knapp et al. 2023).

The probability of *S. nitidibaccatum* occurrence declined with increasing EIV-N CWM values, suggesting its exclusion from nutrient-rich habitats dominated by competitive ruderals or species typical of more advanced stages of secondary succession (Grime 2006). Similarly, in its natural environment, this species avoids competition by inhabiting poor, sandy soils (Särkinen et al. 2015; Knapp et al. 2023) or root and maize crops (Silverside 1977; Puzyrjov 2006). Moreover, this pattern indicates that, while moisture availability is likely to alleviate other abiotic constraints (Crawley 2004; Maestre et al. 2009), high nutrient supply may intensify the role of biotic filters in shaping community assembly (Seabloom et al. 2021). In its introduced range, *S. nitidibaccatum* tends to occupy nutrient-poor sites and field crops, where reduced competition may enhance its performance (Silverside 1977; Bassett and Munro 1985; Puzyrjov 2006; Taab 2021). Similarly, *S. nigrum*, *S. triflorum*, and *S. elaeagnifolium* often grow on poor sandy soils or arable land where competitive pressure remains low (Bassett and Munro 1985; Puzyrjov 2006; Särkinen et al. 2018; Knapp et al. 2023). The negative effects of CWMs of SLA, canopy height, and seed mass, together

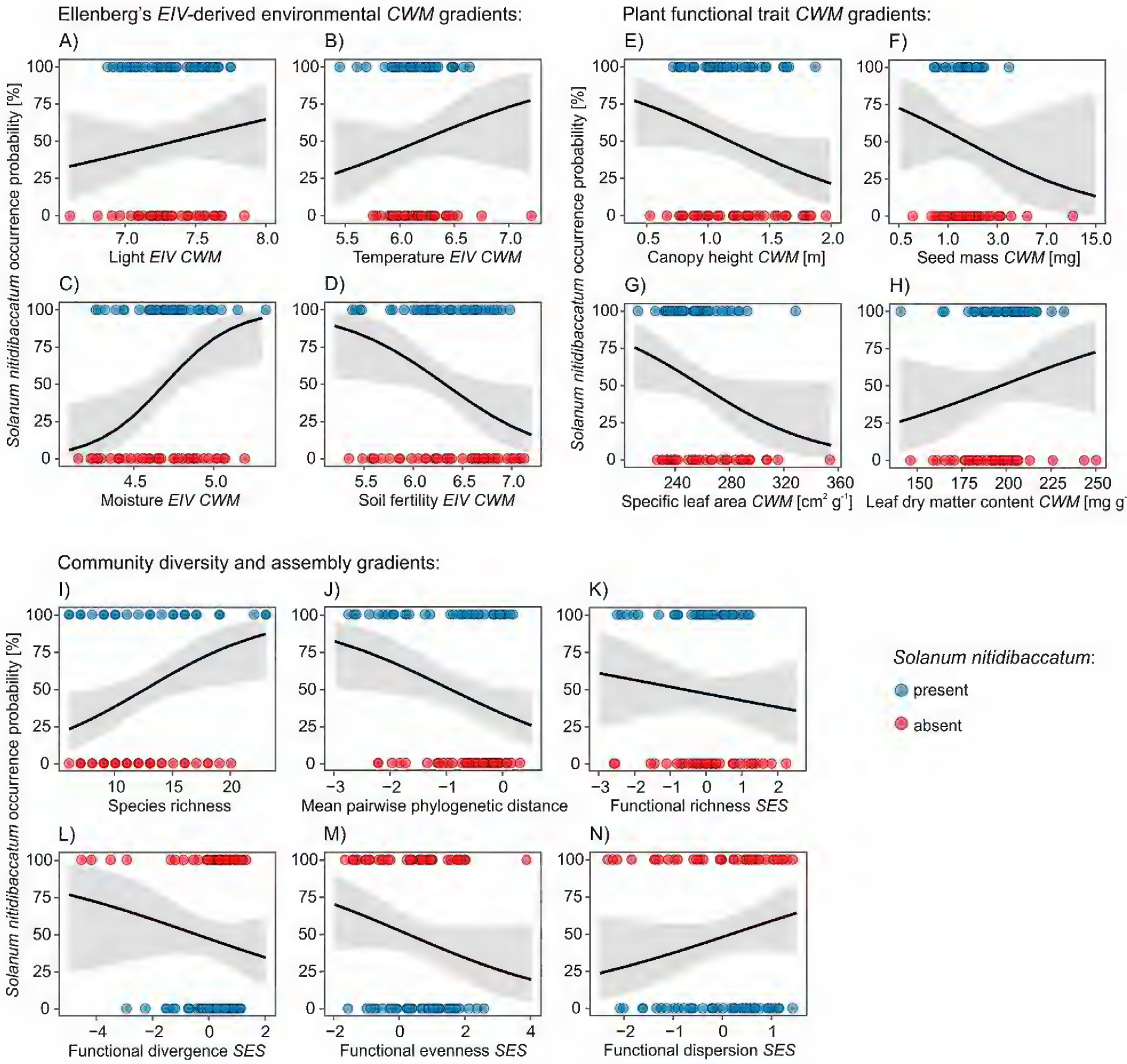

Figure 4. Visualization of the three final generalized linear mixed-effect models (selected using the AICc criterion; Suppl. material 2) predicting the probability of *S. nitidibaccatum* occurrence along Ellenberg's ecological indicator-derived environmental gradients (**A–D**), plant functional trait gradients (**E–H**), and community diversity and assembly gradients (**I–N**). Note log-transformation of the x-axis in (**F**). For model parameters, see Table 3. Abbreviations: EIV – ecological indicator value, CWM – community-weighted mean, SES – standardized effect size.

with the positive effect of CWM of LDMC on the probability of *S. nitidibaccatum* occurrence, may support these patterns, indicating a prevalent role of habitat filtering in shaping its performance. Thus, because *S. nitidibaccatum* germinates late in the season in its introduced range (Del Monte and Tarquis 1997; Taab 2009; Taab and Andersson 2009), it may avoid direct competition with ruderal tall herbs.

Spatio-temporal asynchrony in tall herb canopies may promote *S. nitidibaccatum*

Early senescence of tall-stemmed ruderals with high SLA but low LDMC may reduce canopy persistence, as their leaves are short-lived and their stems lose structural integrity relatively early in the season (Wright et al. 2004; Grime 2006; Poorter et

al. 2009). As a result, temporary light gaps may emerge within the tall-herb canopy. These gaps create windows of opportunity in which the suppressive effect of dense vegetation is relaxed and conditions for the establishment of late-germinating weeds or ruderals are improved (Gioria et al. 2018). Such assemblages characterized by strong phenological asynchrony may amplify this process (Booth et al. 2003; Fenner and Thompson 2005). While some species senesce and open the canopy, others maintain stem and leaf biomass, but never all at once, meaning that canopy closure may be less complete across time (Gioria et al. 2018). In this context, *S. nitidibaccatum* may exemplify a 'join-the-locals' strategy (Lodge et al. 2018; Fridley et al. 2025), thriving by offsetting its life history against that of resident ruderal species. The delayed and prolonged flowering of numerous invasive plant species has been documented on the Iberian Peninsula (Lázaro-Lobo et al. 2025). This likely explains why *S. nitidibaccatum* can occur in assemblages containing species with both low and high values of canopy height, LDMC, SLA, and seed mass (see Fig. 3). This asynchronous canopy turnover could extend the duration and frequency of recruitment windows, increasing the chances that *S. nitidibaccatum* seedlings coincide with favorable microenvironments (Gioria et al. 2018). Being a short-lived colonizer, *S. nitidibaccatum* can thus rapidly exploit these temporal pulses of light and space.

Non-native ruderal species performs better in functionally heterogeneous assemblages

In its introduced range, *S. nitidibaccatum* is able to colonize ruderal vegetation shaped by a wide range of irregular disturbances that vary in frequency and severity (Mogîldea and Biță-Nicolae 2024). Therefore, one may expect that the emergence of fine-scale habitat mosaics can play a pivotal role in enhancing the colonization potential of *S. nitidibaccatum* in urban environments, with functional heterogeneity acting as a key driver of its success. In addition, phylogenetically and functionally similar *Solanum* species are usually found in these types of ecological conditions outside their natural range (Knapp 2018; Särkinen et al. 2018; Krigas et al. 2021).

The probability of *S. nitidibaccatum* occurrence increased with both FDis and species richness, suggesting that communities with a broad range of trait values and high taxonomic diversity provide more opportunities for its establishment. Here, high FDis may reflect species diverging toward broad phenological and stress-tolerance strategies, indicating that niche partitioning could structure community assembly. The higher probability of *S. nitidibaccatum* occurrence in phylogenetically clustered communities corresponds with this pattern. Such assemblages combine closely related species, including early- and late-developing ruderal herbs, tall herbs, and segetal weeds, primarily from Asteraceae, Chenopodiaceae, Poaceae, Fabaceae, and Solanaceae. Under such conditions, not all regions of niche hyperspace may be simultaneously occupied by these functionally heterogeneous species, creating underexploited microsites where late-germinating annuals such as *S. nitidibaccatum* can establish successfully (Gioria et al. 2018). This interpretation may be further reinforced by the negative effect of FEve on the probability of *S. nitidibaccatum* presence, highlighting the strong influence of uneven niche occupation on its performance. High FEve may imply that plants' life-history strategies are represented in similar abundances, effectively saturating available trait hyperspace (Mason et al. 2005; Villéger et al. 2008; Mouchet et al. 2010), and leaving few opportunities for late colonizers (Hejda and de Bello 2013; Gioria et al. 2018). Conversely, low

FEve may reflect clustering around strategies favored by habitat filters (Mason et al. 2005; Villéger et al. 2008; Mouchet et al. 2010), leaving parts of trait hyperspace underrepresented and open to colonization by *S. nitidibaccatum*.

The negative relationship between the probability of *S. nitidibaccatum* occurrence and FRic reflects mechanisms by which the availability of niche hyperspace could become constrained for this species. In communities with low FRic, the trait space tends to be narrow, with few plant strategies represented (Villéger et al. 2008; Hejda and de Bello 2013), leaving unoccupied parts that allow *S. nitidibaccatum* to establish. In contrast, high FRic assemblages support a wider variety of strategies, leading to a more completely filled trait space (Mason et al. 2005; Mouchet et al. 2010) and leaving fewer unoccupied niches that this late-germinating species could exploit (Gioria et al. 2018). Consequently, the probability of *S. nitidibaccatum* establishment decreases with increasing FRic, as communities with higher FRic may provide fewer exploitable niches despite their larger trait hyperspace. This pattern emphasizes that *S. nitidibaccatum* establishment opportunities are determined not by the absolute size of the trait hyperspace, but by the degree to which it is saturated by resident species (Robinson et al. 1995; Higgins and Richardson 2014; Divíšek et al. 2018).

The probability of *S. nitidibaccatum* occurrence was low in assemblages with high FDiv. High FDiv may indicate that species abundances are concentrated toward extreme trait values, characteristic of transient pioneer species colonizing empty niches stochastically rather than being favored by local environmental conditions (Czortek et al. 2021a, 2023; Czortek 2023). Consequently, much of the trait hyperspace may also be inaccessible to *S. nitidibaccatum*, limiting its establishment in strongly pioneer-dominated assemblages. This pattern is consistent with the null niche hypothesis (Czortek et al. 2021a; Ulrich and Zaplata 2023), which assumes that random colonization can generate the apparent functional heterogeneity reflected by high FDiv. Thus, the establishment of *S. nitidibaccatum* appears to depend on deterministic habitat filtering, favoring trait combinations well suited to local environmental conditions, in line with our expectations.

Conclusion

Our results show that the establishment of *S. nitidibaccatum* may be shaped by the high functional heterogeneity of ruderal vegetation developing in a transformed landscape. This process, reinforced by the uneven distribution of plants' life-history strategies within assemblages, could create temporarily underutilized niches providing recruitment opportunities for this late-germinating non-native species. At the same time, habitat filtering could favor particular trait combinations matched to local environmental conditions, further enhancing the success of *S. nitidibaccatum*. This multisided performance suggests that *S. nitidibaccatum* may reveal a high potential to expand into ecologically similar vegetation developing in a wide spectrum of transformed landscapes, including wastelands, post-industrial sites, and croplands with their margins. Thus, the assessed performance of this non-native ruderal suggests that *S. nitidibaccatum* should be treated as revealing high potential to emerge as a problematic invasive weed in the future. The ongoing expansion of *S. nitidibaccatum* and the emergence of other non-native *Solanum* species require further studies, as they may generate ecological and economic impacts that are currently difficult to foresee.

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The authors have declared that no competing interests exist.

Ethical statement

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Author contributions

RP: Conceptualization, Investigation, Data curation, Formal analysis, Methodology, Resources, Visualization, Writing – original draft, Writing – review and editing; PC: Conceptualization, Investigation, Data curation, Formal analysis, Methodology, Resources, Visualization, Writing – original draft, Writing – review and editing.

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Data availability

Raw data are deposited in the Białowieża Geobotanical Station and are available on request.

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Supplementary material 1

Bioclimatic conditions of *Solanum nitidibaccatum* study sites obtained from WordClim v2.1 map data extraction

Authors: Radosław Puchałka, Patryk Czortek

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Supplementary material 2

Most supported (ΔAIC < 2) generalized linear models predicting effects of landscape type and Ellenberg's ecological indicator-derived environmental gradients, plant functional trait gradients, as well as community diversity and assembly gradients on the probability of *S. nitidibaccatum* occurrence

Authors: Radosław Puchałka, Patryk Czortek

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Supplementary material 3

Full species names plotted in Fig. 3

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Data type: pdf

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